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WARM SUMMERS AND RICH BIOTIC COMMUNITIES DURING N-HEMISPHERE DEGLACIATION

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ABSTRACT

Detailed studies on fossil remains of plants or animals in glacial lake sediments are rare. As a result, environmental conditions right at the moment of deglaciation of the large N-Hemisphere ice-sheets remain largely unknown. Here we study three deglacial phases of the Fennoscandian Ice Sheet as a unique, repeated element in a long sediment record preserved at Sokli in northern Finland. We summarize extensive multi-proxy data (diatoms, phytoliths, chironomids, pollen, spores, non-pollen palynomorphs, macrofossils, lithology, loss-on-ignition, C/N) obtained on glacial lake sediments dated to the early Holocene (ca. 10 kyr BP), early MIS 3 (ca. 50 kyr BP) and early MIS 5a (ca. 80 kyr BP). In contrast to the common view of an unproductive ice-marginal environment, our study reconstructs rich ecosystems both in the glacial lake and along the shores with forest on recently deglaciated land. Higher than present-day summer temperatures are reconstructed based on a large variety of aquatic taxa. Rich biota developed due to the insolation-induced postglacial warming and high nutrient levels, the latter resulting from erosion of fresh bedrock and sediment, leaching of surface soils, decay of plant material under shallow water conditions, and sudden decreases in lake volume. Aquatic communities responded quickly to deglaciation and warm summers and reflect boreal conditions, in contrast to the terrestrial ecosystem which responded with some delay probably due to time required for slow soil formation processes. Birch forest is reconstructed upon deglaciation of the large LGM ice-sheet and shrub tundra following the probably faster melting smaller MIS 4 and MIS 5b ice-sheets. Our study shows that glacial lake sediments can provide valuable palaeo-environmental data, that aquatic biota and terrestrial vegetation rapidly accommodated to new environmental conditions during deglaciation, and that glacial lake ecosystems, and the carbon stored in their sediments, should be included in earth system modeling.

Keywords: glacial lake sediment, ice-marginal environment, climate, ecosystem response, carbon storage, Fennoscandian Ice Sheet

1 Introduction

Glacial lake sediments are a persistent element in the geological record (Carrivick and Tweed, 2013; Lunkka et al., 2015) and former extents of glacial lakes have been mapped in different regions globally (Lundqvist, 1972; Björck, 1995; Dyke, 2004; Glasser et al., 2016). Particularly the drainage of large glacial lakes has received significant attention as it has the potential of influencing ocean circulation and climate on a global scale (Broecker and Denton, 1990; Barber et al., 1999).

Extensive ice-marginal retreat in the Fennoscandian and Laurentide Ice Sheets occurred at the last peak of high-latitude summer insolation around ca. 10 kyr cal BP (Dyke, 2004; Stroeve et al., 2016). The postglacial warming allowed for the production of large amounts of meltwater and, with the land-surface inclined towards the retreating ice-fronts due to isostatic depression, glacial lakes were formed extensively (Fig. 1). Although the sediments deposited in these lakes and fossil remains stored in them form a potential natural archive for palaeo-environmental and -climatic studies, the biotic content of glacial lake sediments has been rarely analyzed in detail. The lack of fossil analysis on glacial lake sediments is probably due to the generally low fossil content and often broken/corroded nature of fossil remains (e.g. Lunkka et al., 2015), making the analysis particularly time-consuming. Also, fossil remains are often considered as redeposited from older deposits as the ice-marginal environment is classically interpreted as harsh and unproductive (e.g. Stroeve et al., 2016). The difficulty of recovering the minerogenic glacial lake sediment at the base of Holocene peat or gyttja sequences with the help of conventional hand-coring adds yet another reason for the lack of studies on these sediments.

The north-eastern margin of the Fennoscandian Ice Sheet receded from the Sokli basin in northern Finland (Fig. 1) several times during Marine Isotope Stages (MIS) 5 to 1. Glacial lake deposits dated to early MIS 5e, 5a, and 3 and the early Holocene are found here in stratigraphic sequence with glacial till beds and non-glacial lacustrine and fluvial deposits. During each deglaciation episode there was a progression of lake stages associated with deglaciation (stage 1), maximum extent of the glacial lake (stage 2), and glacial lake drainage (stage 3). The Sokli sequence uniquely preserves lake sediments from four deglaciation episodes due to a non-typical bedrock setting combined with frozen-bed conditions at the base of the Fennoscandian Ice Sheet (Helmens et al., 2007a, and references therein).

The Sokli sedimentary sequence provides an exceptional opportunity to study the ice-marginal environment during the retreat of a continental ice-sheet as a repeating element in the Late Quaternary geological record at a single site. We here integrate multi-proxy data (diatoms, phytoliths, chironomids, pollen, spores, NPP's (non-pollen palynomorphs), macrofossils, lithology, LOI (loss-on-ignition), C/N) that are available for the glacial lake sediments in the Sokli basin dated to the early Holocene (Shala et al., 2014a, 2014b, 2017) and early MIS 3 (Engels et al., 2008; Bos et al., 2009; Helmens et al., 2009), and further compare this extensive data-set with newly obtained data for multiple proxies from the glacial lake sediments of early MIS 5a age. The overall coarse-grained glacial lake sediment found at the base of the MIS 5e gyttja deposit contains very few fossil remains (Pliikk et al., 2016) and is not included in this study. The aim of our study is to reconstruct in detail biota in the glacial lake, along its shores and on the surrounding land, as well as successive developments in these ecosystems upon deglaciation and glacial lake evolution, for a series of Late Quaternary deglaciation episodes at the same site. Furthermore, the multi-proxy data are used to make climate inferences. Our study provides valuable paleo-environmental data and new understanding on the aquatic and terrestrial productivity of the ice-marginal environment during N-Hemisphere deglaciation.

2 Environmental and stratigraphic setting

2.1 The study site

The Sokli site is situated in the northern boreal forest of north-eastern Finland (lat. 67°48' N, long. 29°18' E, elevation ca. 220 m a.s.l.) and on the main water divide that separates drainage into the Barents and White Seas to the east and the Baltic Sea to the southwest (Fig. 1). Bedrock in the region is Precambrian Shield with the exception of the immediate surroundings of the study site which is underlain by a Paleozoic magma-intrusion known as Sokli Carbonatite Massif (Fig. 2B). The Sokli wetland (Sokliaapa) is drained by the Sokli rivulet (Soklioja), the latter flowing south-westwards into the Yli-Nuortti river. Within the Sokli basin, Lake Loitsana occupies a depression associated with a NW-SE trending esker chain.

Present climate at Sokli is cold boreal with mean July and February temperatures at 13°C and -14°C, respectively; mean annual precipitation amounts to 500-550 mm (Drebs et al., 2002). Lakes in the area are ice-covered between October and end of May. Birch (*Betula pubescens* and *B. pendula*), pine (*Pinus sylvestris*) and spruce (*Picea abies*) are the dominant tree species. Mires of the aapa-type (i.e. a patterned fen) with *Sphagnum* spp., *Rubus chamaemorus*, Ericales, *Betula nana* (dwarf birch), *Salix* spp. and *Carex* spp. are extensively present in the region. Spruce reaches its northern limit some 100 km north of Sokli. Farther north, pine forest predominates, succeeded northwards and upwards by birch-pine forest and then sub-arctic birch forest. The forest limit, which is situated some 300 km north of Sokli, is formed by the polycormic mountain birch *B. pubescens* subsp. *czerepanovii*, syn. *tortuosa*. The vegetation of the tundra region beyond the forest limit is low-arctic dwarf-shrub tundra dominated by *B. nana* and Ericales.

2.2 Late Quaternary stratigraphy in the Sokli basin

An unconsolidated sedimentary sequence up to ca. 30 m in thickness, including several organic units and till beds, is present in the central part of the Sokli Carbonatite Massif where two main fault zones cross (Fig. 2A, B). The unusually long Sokli sediment record, which spans the last ca. 140 kyr, has been protected from glacial erosion due to its sheltered position in a steep depression formed in the deeply-weathered rocks of the Sokli Massif.

The composite lithological log in Figure 2A is based on a series of boreholes collected between 1996-2010 (Fig. 2B) and is an updated version from lithological columns earlier presented in Helmens et al. (2000, 2007a). The Sokli sediments have been dated by AMS ¹⁴C dating on macrofossils of terrestrial plants, TL and IRSL dating, and OSL dating on quartz using SAR dose protocol (Helmens et al., 2000, 2007a; Alexanderson et al., 2008). OSL dates on quartz yielded large standard errors mainly due to small sample sizes, relatively poor luminescence characteristics, and uncertainties in dose-rate determinations. The OSL ages are, however, in sequence and (together with ¹⁴C ages) group according to stratigraphic units (Fig. 2A); furthermore, the absolute chronology is in agreement with earlier made

land-sea comparisons (Fig. 2C; Helmens *et al.*, 2000, 2007a; Alexanderson *et al.*, 2008). The stratigraphy in the Sokli basin (Fig. 2A, right side) is according to Helmens (2014).

A diatom gyttja deposit up to 9 m in thickness, and dated to the Eemian Interglacial (MIS 5e), stretches as a marker horizon near the base of the Sokli basin infill (Plikk *et al.*, 2016; Fig. 2). The diatom gyttja overlays coarse-grained glacio-lacustrine sediment resting on till (MIS 6; Ilvonen, 1973). A sand and gravel deposit of fluvial origin (MIS 5d) separates the MIS 5e lake sediment from sandy gyttja that was deposited in an oxbow lake during MIS 5c (Helmens *et al.*, 2012). The upper part of the Sokli sedimentary sequence consists of till interlayered with two additionally well-sorted, fine-grained lacustrine sequences (MIS 5a and MIS 3). The deposition of glacio-lacustrine silt and clay in early MIS 5a was followed by the accumulation of gyttja (this study). The glacio-lacustrine sediment of early MIS 3 age is capped by till (Helmens *et al.*, 2009). Lake Loitsana holds a 7m-thick gyttja deposit underlain by a glacio-lacustrine deposit of early Holocene age (Shala *et al.*, 2014a, 2014b). Glaciation of the Sokli basin is dated to MIS 5b, MIS 4 and late MIS 3-2 (Helmens *et al.*, 2007a).

2.3 The Sokli Ice Lake

The Late Quaternary glacial lake sediments preserved in the Sokli basin were deposited in the Sokli Ice Lake (Fig. 1). Figure 3 gives a schematic representation of the evolution of the later stages of the Sokli Ice Lake, i.e. from the moment of deglaciation of the Sokli site (Lake Stage 1) until its final drainage through the Nuortti canyon (Lake Stage 3). Glacier meltwater was trapped between the hills of the Värriö tunturi and the retreating ice-margin during the early stages of the glacial lake (Johansson, 1995).

The ice-marginal retreat pattern in Figure 3 is guided by NW-SE oriented eskers that are dated to the last deglaciation in the early Holocene (Johansson, 2007; Shala *et al.*, 2014a). Importantly, a similar evolution of these final stages of the Sokli Ice Lake has been reconstructed for early MIS 3 (Helmens *et al.*, 2009) based on N-S trending, till-covered eskers in the region dated by OSL at 65 ± 13 kyr BP (Johansson, 2007). The direction of ice-marginal retreat in early MIS 5a was to the northwest (Johansson, 1995) and, also during this deglaciation episode, the glacial lake evolution was probably similar as during the early Holocene. The reconstruction in Figure 3 is based on geomorphologic (e.g.

meltwater channels) and DEM (Digital Elevation Model) data and corresponds to the one originally presented in Johansson (1995). As the area invoked in the glacial lake reconstruction is relatively small (ca. 30 x 30 km), possible errors generated due to non-uniform isostasy are considered to be insignificant (cf. Jansson 2003).

During each deglaciation episode, the Sokli Ice Lake varied in surface area and water depth depending on the position of the ice-front and the location of spillways/overflow sites (Fig. 3). During Lake Stages 1 and 2, the level of the glacial lake was controlled by the col at the head of the Törmäoja canyon which has a present elevation of 240 m. The glacial lake reached its maximum spatial extension during Lake Stage 2. Opening of the Nuortti canyon resulted in partial (Lake Stage 3; col at 220 m elevation) and final drainage of the Sokli Ice Lake.

3 Methods

A total of 2 m of glacial lake silts and clays, below 7 m of gyttja, was retrieved with the Russian peat corer from ice-covered Lake Loitsana. The 1-2 m thick early MIS 3 and MIS 5a glacial lake deposits, which underlie the LGM (Last Glacial Maximum) till, were recovered using heavy-equipment percussion drilling from the frozen surface of the Sokli wetland. Methods used for multi-proxy analysis on the sediments of early MIS 5a age follow those applied to the glacial lake sediments of early MIS 3 and early Holocene age. The latter are presented in Helmens et al. (2009) and Shala et al. (2014a, 2014b) (siliceous microfossils and LOI); Engels et al. (2008) and Shala et al. (2014b) (chironomids); Bos et al. (2009) and Shala et al. (2014b, 2017) (pollen/spores/NPP's and macrofossils); and Shala et al. (2014b) (C/N). For all three time-slices (early Holocene, MIS 3 and 5a), diatom and chironomid diversities are calculated using Hill's N_2 (effective number of occurrences; Hill, 1973).

A minimum of 500 diatom valves, 50 chironomid head capsules and ca. 400 terrestrial pollen grains were identified in each sample from the early MIS 5a glacial lake deposit. The sample size for the macrofossil analysis was mainly 10-15 cm³. Furthermore, we submitted two samples from gyttja found overlying the early MIS 5a deglacial sediment for AMS ¹⁴C dating.

4 Results and Discussion

4.1 Timing and duration of the Sokli Ice Lake

¹⁴C dating on seeds of tree birch encountered in the youngest glacial lake deposit has provided an age of ca. 10.5 kyr cal BP for the last deglaciation of the Sokli basin (Shala et al., 2014a, 2014b). This date is in accordance with the early Holocene deglaciation chronology for north-eastern Fennoscandia as presented in Johansson (2007) and Stroeve et al. (2016). It also shows that the *Betula* seeds occur in-situ, i.e. they are not reworked from older deposits. The in-situ preservation of fossil remains in the glacial lake sediment is further demonstrated by ¹⁴C ages on wood from the early MIS 3 sediment sequence (Helmens et al., 2000, 2007b) which are in line with OSL dating results (Alexanderson et al., 2008; Figs. 2 and 4B). The latter deglaciation episode probably occurred at ca. 53 kyr BP during prominent Greenland Interstadial (GI) 14 (Helmens et al., 2007b; Helmens and Engels, 2010). New ¹⁴C datings of macrofossils from gyttja that overlies the oldest glacial lake deposit gave, as expected, infinite ages (Table 1). This episode of deglaciation has been earlier dated to early MIS 5a based on OSL dating of glacio-fluvial sand and gravel, that occur beneath the glacial lake sediment, at ca. 80 kyr BP and of minerogenic sediment at the top of the overlying gyttja at ca. 74 kyr BP (Alexanderson et al., 2008; Figs. 2 and 4C).

The duration of the Sokli Ice Lake following the last deglaciation of the Sokli site is estimated at less than 100 yr (Johansson, 2007; Stroeve et al., 2016; Fig. 3). A duration of some 400 kyr is inferred based on ¹⁴C dating evidence from the early Holocene glacial lake deposit in the Sokli basin (Shala et al., 2014a, 2014b) and counting of the distinct, possibly annual laminae in the glacial lake sediment of early MIS 3 age (Helmens et al., 2009). However, the 50 to 100-year error margins on the ¹⁴C dates (Fig. 4A), and the large spread in calendar ages for the earliest Holocene, hamper a detailed age determination for glacial lake duration.

4.2 Aquatic and telmatic ecosystem changes in the ice-marginal environment during deglaciation

The evolution of the Sokli Ice Lake as depicted in Figure 3 can be clearly traced in the sediment sequence of each deglaciation episode (early Holocene, MIS 3 and 5a; Fig. 4). The ice-marginal retreat during Lake Stages 1 and 2 is recorded by an upward-fining sequence of sandy and silty sediment grading into rhythmically laminated silts and clays at the base of each glacial lake sequence. Following the decrease in level and size of the glacial lake associated with the opening of the Nuortti canyon (Lake Stage 3), silts (early Holocene) and silts grading into sandy sediment (early MIS 3 and 5a) were deposited at the coring-sites. Lacustrine sedimentation is recorded to continue with the accumulation of organic silts followed by gyttja in the Sokli basin during early MIS 5a, and gyttja in Lake Loitsana in the early Holocene. The early MIS 3 glacial lake sediments were found to be covered by till. Furthermore, the Sokli Ice Lake evolution has been traced in XRF-based geochemical data available for the early Holocene glacial lake sediment (Shala et al., 2014a). The latter shows a decrease in sediment input enriched in elements (Ca, S and Nb) typical for the local bedrock (Sokli Carbonatite Massif) during Lake Stage 2, i.e. when the Sokli Massif became entirely submerged in the expanding glacial lake (Fig. 3).

The biotic proxy diagrams obtained from the early Holocene (Fig. 4A), early MIS 3 (Fig. 4B) and early MIS 5a glacial lake sediments (Fig. 4C) reveal marked compositional shifts in biotic assemblages in concordance with the changes in size and depth of the Sokli Ice Lake. This shows that biota responded quickly to environmental changes during deglaciation. It also provides further support for the in-situ preservation of fossil remains. Although the biotic data obtained for the different deglaciation episodes share many similarities, fossil assemblages and successive developments appear to be influenced by actual lake depth. Overall deepest lake conditions are reconstructed for early MIS 5a, and shallowest waters during the early Holocene. This can be expected due to continuing infilling of the Sokli basin and progressive lowering of the glacial lake outlet channels resulting from erosion. Below, the biotic records will be used to reconstruct in detail the aquatic and telmatic ecosystem composition in and along the shore of the Sokli Ice Lake during its evolution.

4.2.1 Glacial Lake Stages 1 and 2

The fossil content and diversity of fossil remains (expressed by e.g. Hill's N_2 values for diatoms and chironomids) increase, both during the early Holocene (Fig. 4A) and early MIS 3 deglaciation episodes (Fig. 4B), with increasing distance of the ice-margin from the coring-site (Lake Stages 1-2 in Fig. 3). The overall meagre fossil content of the Lake Stage 1-2 sediments of early MIS 5a age (Fig. 4C) most probably result from deep water conditions (suggested by relatively high planktonic diatom percentages) and long distance to shore. Furthermore, C/N values (only measured for the Holocene (Fig. 4A)) gradually drop during Lake Stages 1-2 suggesting an increased in-lake productivity. It is less-likely that the low C/N values in the latter part of Lake Stage 2 result from a decreased contribution of higher plants since seeds of *Carex* and high pollen percentages of Cyperaceae and *Salix* indicate an expansion in the wetland zone close to the coring-sites. In general, high C/N ratios (> 10) indicate input of organic matter from higher plants (littoral/wetland/terrestrial), and low ratios (< 10) reflect input from phytoplankton (Wetzel, 2001).

Turbulent waters and turbid water conditions occur close to ice-margins and significantly decrease primary productivity (Henley et al., 2000). Also, the fossil record in the coarse-grained ice-marginal sediment at the base of the studied sequences (Lake Stage 1) can be expected to be diluted due to high sedimentation rates (Risberg et al., 1999) and plant/animal remains to be more easily destroyed in this high-energy environment.

Chironomids that are recorded among the first colonizers of the Sokli Ice Lake during all three time-slices (early Holocene, MIS 3 and 5a) are the deep-water taxa *Heterotrissocladius maeaeri*-type, *Tanytarsus lugens*-type and *Procladius*. *H. maeaeri*-type is reported to have dominated the deep waters of the late-glacial Baltic Ice Lake in southern Finland (Fig. 1; Luoto et al., 2010). Diatoms were mostly Fragilariaceae and *Aulacoseira*. Fragilariaceae is a group of taxa that is characterized as pioneering and opportunistic, since they colonize quickly, have high reproduction rates and are more adaptive to a changing environment (Risberg et al., 1996; Lotter et al., 1999). The encountered planktonic *Aulacoseira* species (*A. ambigua*, *A. subarctica*, *A. alpigena*) are all heavily silicified and most probably reflect a large influx of Si into the glacial lake and enhanced levels of turbulence. A high Si-level is

further suggested by findings of *Tetracyclus glans* (Michel et al., 2006). Statoblasts of the bryozoan *Fredericella indica* (Økland and Økland, 2001) and high abundances of pooid phytoliths and Tertiary diatoms in the sediment indicate wave action and significant shore erosion. Tertiary diatoms are exemplified by species like *Pliocaenicus costatus*, a relict freshwater taxon from the Pliocene, and *Paralia sulcata* of marine-origin, their robust structure allowing for multiple phases of re-working (Helmens et al., 20009, and references therein). The pioneering algal *Botryococcus braunii*, algal type T.225 (van Geel et al., 1989) and the cladoceran *Daphnia* (water-flea; recorded by ephippia) are additionally well-represented among the first lake colonizers.

Occurrences of the diatom taxa *Epithemia adnata* and *Rhopalodia gibba* in the upper part of the Lake Stage 2 sediment of early Holocene age suggest pH values exclusively above 7 (van Dam et al., 1994). High abundances of ostracod remains indicate enhanced Ca-concentrations. This lake water chemistry mostly probably resulted from rapid leaching of carbonates and other soluble minerals from surface soils shortly after deglaciation (Engstrom et al., 2000). An enhanced level of nutrients in the glacial lake during the latter part of Lake Stage 2 in early MIS 3, and particularly during early MIS 5a, is further suggested by relatively high percentage values of *Stephanodiscus* species (*S. medius*, *S. minutulus*, *S. neoastraea*, *S. alpinus*).

Although the recording of the bryozoan *F. indica* suggests stony shores with sparse aquatic vegetation (Økland and Økland, 2005), macrofossils, pooid phytoliths and pollen indicate the presence of the herbs *Rorippa palustris*, *Filipendula* and grasses (e.g. *Glyceria lithuanica*) as well as *Empetrum nigrum*, *Carex*, *Juncus* *Equisetum* and *Sphagnum* in local shore or wetland habitats (i.e. telmatic habitat) along the glacial lake shoreline.

4.2.2 Glacial Lake Stage 3

The local establishment of diverse aquatic and telmatic communities is recorded in the silty glacial lake sediments of Lake Stage 3. This stage followed the opening of a new spillway which resulted in a drastic decrease in water depth and size of the Sokli Ice Lake (Fig. 3). The margin of the Fennoscandian Ice Sheet during Stage 3 was situated at a distance of less than 10 km from the coring-site (i.e. before

deglaciation of the Nuortti canyon in Fig. 3). The amount of macrofossils in lake sediments is strongly influenced by taphonomic factors, e.g. with a close location of the shoreline sharply increasing macrofossil abundances at the coring-site (Hannon and Gaillard, 1997; Välranta, 2006), and macrofossils are distinctly more abundant in the Lake Stage 3 sediment, particularly in the early Holocene. Below, the Lake Stage 3 aquatic and telmatic ecosystems will be discussed separately for the three deglaciation episodes.

Fossil remains in the early Holocene deposit (Fig. 4A) reflect a shallow lake and even further shallowing, accompanied by an extension in the wetland zone (macrofossils of *Carex*, *B. nana*, *Vaccinium*, *Typha* and *Ranunculus* sect. *Batrachium*), higher up in the Stage 3 silts. Characteristic is the high representation in the macrofossil record of the shallow-water plant *Callitriche cophocarpa/hermaphroditica*, the bryozoan *Plumatella repens* and *Daphnia*. Also, various littoral chironomid taxa (*Polypedilum nubeculosum*-, *Microtendipes pedellus*-, *Dicrotendipes nervosus*-type) are recorded. A large variety of *Potamogeton* species (*P. berchtoldii*, *P. filiformis*, *P. friesii*, *P. obtusifolius*, *P. pectinatus*), aquatic Nymphaeaceae (*Nymphaea*, *Nuphar*), and the bryozoan *Cristatella mucedo* are additionally well-represented in the upper part of the silt deposit. The pioneering, narrow-leaved *Potamogeton* species thrive in shallow (0.1-1.5 m) water depths. *C. mucedo* (if produced locally) suggest more coloured water with less wave action than *F. indica* (Økland and Økland, 2005). Simultaneously to the trend in lake shallowing, rising nutrient levels are suggested by increasing abundances of the chironomid taxon *Endochironomus albipennis*-type (Møller Pillot, 2009). The occurrences of *C. mucedo*, Nymphaeaceae and *Typha* indicate boreal conditions. In contrast to these rich biotic communities, diatom assemblages in the early Holocene Stage 3 sediment are largely dominated by *Staurosira construens* var. *venter*, showing peak values reaching > 85%. This might reflect the littoral and periphytic (growing on plants) habitat preferences of this diatom species and/or tolerance to poor light conditions (Bigler et al., 2003), the latter possibly resulting from erosion of the adjacent esker.

Shallowing of the glacial lake and accompanying rising nutrient levels are recorded in detail in the thick early MIS 3 silty deposit. Initially, *F. indica* (Økland and Økland, 2005) and the chironomid taxon *Ablabesmyia* (Vallenduuk et al., 2007) suggest moderate nutrient availability. Subsequently, nutrient levels increase as indicated by high percentage values for *E. albipennis*-type combined with

occurrences of *P. friessi* and the macro-algae *Nitella*. The appearance of the cladoceran *Simocephalus* in the upper sandy part of the deposit suggests shallow, open water, eutrophic conditions and dense stands of vegetation (van Geel et al., 1983). Strongly reduced water depths during deposition of the upper sandy silts of Stage 3 are further indicated by enhanced values for the shallow-water algae *Spirogyra* and the littoral diatom taxon *Staurosirella pinnata*, as well as a distinct extension in the wetland zone. The latter is recorded by high abundances of bryophyte leaves, seeds of *Carex*, *Juncus*, *B. nana* and *E. nigrum*, increased percentage values for Cyperaceae pollen and a near continuous registration of hyphopodia of *Clasterosporium caricinum*, i.e. a fungus that parasitizes on *Carex* (van Geel et al., 1983).

Fossils in the silty Glacial Lake Stage 3 sediment of early MIS 5a age include macro-remains of *P. repens*, *Callitriche* (*C. cophocarpa*, *C. hermaphroditica* *C. hamulata*), narrow-leaved *Potamogeton* (including *P. compressus*) and the shallow-water plant *Ceratophyllum*. Characteristic is the combined appearance of *Tanytarsus pallidicornis*- and *Psectrocladius sordidellus*-type, i.e. chironomid taxa presently common in the sublittoral and littoral zones of boreal lakes mostly found living among *Phragmites* stands (Luoto, 2010). Nutrient availability was overall high as indicated by occurrences of *E. albipennis*-type, *Chironomus plumosus*-type (Brooks et al., 2001) and a high representation of *Stephanodiscus* among the diatoms. The enhanced nutrient level, and high chironomid species diversity (high Hill's N_2 values), might be related to inflow of running water close to the coring-site as also has been recorded in the MIS 5d-c deposit in the Sokli basin (Engels et al, 2010). Inflow of water is indicated by relatively high abundances of stream-inhabiting chironomid taxa (e.g. *Eukiefferiella* and *Rheocricotopus*) as well as the type of lamination of the silty deposit, i.e. laminae of varying grain-sizes (clay to fine sand) and thicknesses. Similar as during the early Holocene and MIS 3, a strong reduction in water depth during deposition of the uppermost sandy part of the MIS 5a silt deposit is reflected in the fossil record (littoral *M. pedellus*-type and *S. pinnata*; macrofossils of *Carex*, *Salix*, *B. nana*).

Interestingly, the diatom *Aulacoseira granulata* var. *angustissima* appears with peak values in the upper sandy sediment of Lake Stage 3 both during early MIS 5a and MIS 3 and, together with increased representations of the diatom taxa *Staurosirella leptostauron*, *Diploneis elliptica* and *Amphora libyca*, reflect alkaline waters with high Ca-concentrations (Gómez et al., 1995; Jones et al., 2004). This lake

water chemistry was recorded in the early Holocene glacial lake sequence already during the relatively shallow-water Lake Stage 2. It is possible that the glacial lake volume during early MIS 3 and 5a became only reduced enough during Lake Stage 3 in order for alkaline water conditions to be established.

4.2.3 Early Loitsana and Sokli lakes

The early Holocene sandy gyttja deposited in Lake Loitsana contains relatively high fossil abundances of the chironomid taxa *Cricotopus intersectus*- and *Cricotopus cylindraceus*-type. These are typical littoral taxa with an affinity for plants (Brooks et al., 2007; Luoto, 2010) and their occurrences might be related to an influx of insect and plant remains (e.g. *Equisetum* tissue) by running water. Particularly stream-inhabiting chironomids (e.g. *Rheotanytarsus*, *Eukiefferiella*, *Rheocricotopus*), but also rheophilic diatom taxa (e.g. *Meridion circulare*, *Amphora pediculus*), indicate inflow of running water nearby the coring-site. *Corynocera ambigua*, which has a complex ecology (Brodersen and Lindegaard, 1999), dominates the chironomid assemblage in the MIS 5a lake deposit in the Sokli basin. Nutrient levels were high both in the early Loitsana and Sokli lakes (*E. albipennis*-type, *C. plumosus*-type, *Stephanodiscus parvus*). This might have resulted from morphometric eutrophication (Hofmann 1998), i.e. a condition created by a reduction in lake volume. In our study, the latter occurred when the Sokli Ice Lake fully drained and lacustrine sedimentation continued in small depressions within the Sokli basin.

4.3 MIS 3 ice-sheet dynamics

The glacial lake sequences of early Holocene, MIS 3 and MIS 5a age reveal remarkably similar assemblages and successions in aquatic and telmatic biota, however, some additional, special features are shown by the early MIS 3 glacial lake deposit. This most probably relates to different levels of ice-sheet dynamics upon deglaciation. First, the glacial lake sediment of early MIS 3 age is interlayered throughout the sequence with distinct clay laminae suggesting a continuing influence of the ice-sheet on lake deposition, even in the case of a distal position. Secondly, the sediment and fossil record seems to

register a glacier re-advance phase which intersected the shallow Glacial Lake Stage 3. The latter is demonstrated by the re-occurrence of deep water (increases in tycho-planktonic diatom taxa and the deep-water chironomid taxon *T. lugens*-type), a large lake-size (*Aulacoseira islandica*; Serreyssol et al., 2009), oligotrophic lake water conditions (*Cymbella aspera*; Krammer and Lange-Bertalot, 1986) and significant shore erosion (> 50 % of phytoliths) (Fig. 4B). Re-advances of the ice-margin are commonly recorded in glacial lake sediment sequences and are not necessarily climate-driven (Carrivick and Tweed, 2013). Striking also is the co-occurrence of peak abundances of *Procladius* with a large variety of algae (*B. braunii*, *Pediastrum*, *Tetraedon* cf. *minimum*, *Zygnema*, *Spirogyra*, T.225; high diatom-inferred Hill's N_2) in the finely laminated clayey sediment at the end of Stage 2. This might reflect density stratification, a process typical for glacial lakes (Carrivick and Tweed, 2013, and references therein) in which sediment-loaded cold meltwater extends below warmer and more transparent river-fed water. The river-fed water probably favoured a diverse algal community. *Procladius*, which is abundant during this phase, is a ubiquitous chironomid taxon with a wide environmental tolerance including turbid water inflows (Greffard et al., 2012) and is found in lakes with a large variability in limnological conditions, such as hypolimnetic oxygen availability and water temperature (Brodersen et al., 2004). In addition to these features, the till bed, and overlying glacio-fluvial gravels and sands, at the base of the early MIS 3 deglacial sediment sequence shows large chunks of organic debris reworked from the Eemian Interglacial (MIS 5e) gyttja in the Sokli basin (Helmens et al., 2000). All these features together suggest active, warm-based ice in the course of early MIS 3 deglaciation.

4.4 Terrestrial vegetation in the ice-marginal environment during deglaciation

Pollen and macrofossil remains found in the glacial lake sediments further allow a detailed reconstruction of terrestrial vegetation during the different episodes of deglaciation. Numerous seeds of birch trees and pollen percentage values for *Betula pubescens/pendula* of up to 80 % in the shallow Glacial Lake Stage 3 silts of early Holocene age (Fig. 4A) indicate the presence of birch forest on the land adjacent to the Sokli Ice Lake (Shala et al., 2017). Birch trees already bordered the glacial lake during Stage 2 (macrofossils present) and possibly Stage 1, i.e. in close proximity to the ice-margin.

Macrofossils are overall scarce in the latter sediments, probably due to the large lake size and long distance to shore. Moreover, the large contribution of grasses to the pollen sum, which for a major part might be derived from local shore habitats (high abundances of phytoliths), inhibits a precise pollen-based reconstruction of the terrestrial vegetation during Lake Stages 1 and 2.

B. pubescens/pendula and *Pinus* are represented by pollen values of 30-50 % and 20 %, respectively, in the glacial lake sediments of early MIS 3 and MIS 5a age (Fig. 4B-C). Whereas *B. pubescens/pendula* dominates the pollen assemblages in modern calibration samples from the sub-arctic birch forest in northern Fennoscandia, birch pollen percentages drop at the expense of pine pollen north of the birch tree-line (Aario, 1940; Prentice, 1978). The increase in representation of pine relative to birch occurs as the forest thins out, and *Pinus* pollen with its greater dispersal capability is being blown in from the south. Therefore, the modern calibration data suggests the presence of tundra vegetation on recently deglaciated terrain during early MIS 3 and 5a. According to Bos et al. (2009), the tundra vegetation during early MIS 3 appears to have been remarkably similar to the present-day tundra in northern Fennoscandia. Seeds of tree birch in the early MIS 5a glacial lake sediment indicate the presence of birch trees in the tundra vegetation, and *B. pubescens/pendula* pollen percentage values rising to 80 % in the overlying gyttja deposit registers the local establishment of birch forest. Pine forest with larch is recorded in the younger part of the MIS 5a gyttja deposit (N. Kuosmanen, unpublished data). Pollen and macrofossil data from interstadial organic-bearing sediment in northern Finland, dated to MIS 3, register birch forest and the local presence of pine trees (Sarala et al., 2016).

Betula spp. are fast immigrants due to the advantage of an abundant production of wind-dispersed fruits, rapid reproductive rates, fast growth rates and a young reproductive-maturity age (Birks, 1986). Furthermore, rapid migration of trees over the deglaciated land was probably facilitated by the northern location of glacial plant refugia (Välranta et al., 2011; Tsuda et al., 2016). The existence of boreal tree populations in northerly small pockets of environmentally favorable conditions, in some cases close to the edge of the LGM ice-sheet, is being suggested by evidence from e.g. macrofossil charcoal assemblages and ancient DNA (Willis and van Andel, 2004; Parducci et al., 2012). However, while aquatic biota in the glacial lake show a mostly boreal character (see section 4.2), vegetation on land was sub-arctic in nature probably due to time needed for soil forming processes (Välranta et al., 2015).

Interestingly also, our study shows that forested conditions were achieved in the ice-marginal environment during the early Holocene, whereas more open tundra vegetation seems to have characterized this environment during early MIS 3 and 5a. This might be the result of the relatively slow melting of the large LGM ice-sheet, allowing tree birch to migrate in congruent pace with the retreating ice-margin.

4.5 Climate during deglaciation

There is overwhelming evidence in the fossil record from the early Holocene, MIS 3 and MIS 5a glacial lake sediments at Sokli for warm summers during deglaciation. This result is in accordance with high Milankovitch-forced summer insolation at high latitudes during all three time intervals (Berger and Loutre, 1991; Fig. 2).

Table 2 summarizes estimates of mean July air temperature (T_{jul}) for the three deglaciation episodes based on macrofossil and chironomid remains. Aquatic and telmatic plant indicator taxa identified in the macrofossil records are given in the table together with (in parenthesis) lowest required T_{jul} for current species presence in Finland (following Valiranta et al., 2015; Shala et al., 2017). Additionally, chironomid taxa with warm temperature optima (i.e. warmer-than-today) are indicated; the optima are based on the distribution patterns of chironomid taxa in the Finnish chironomid-temperature calibration data-set (Luoto et al., 2014a, 2014b). The presence of these warm-indicating plant and chironomid taxa (Table 2), as well as the quantitative chironomid-inferred T_{jul} records for early MIS 3 (Engels et al., 2008), the early Holocene (Shala et al., 2017), and early MIS 5a (T. Luoto, unpublished data), indicate mean July air temperatures similar (13 C) or higher-than-today during all three deglaciation episodes. Highest T_{jul} (ca. 15-15.5 C) are inferred for the early Holocene deglacial episode (Table 2; Shala et al., 2017). Furthermore, the aquatic and littoral plant macrofossil assemblages encountered in the glacial lake sediments consistently suggest boreal conditions in the ice-marginal environment (Bos et al., 2009; Valiranta et al., 2015; Shala et al., 2017; this study).

Warm summers in Fennoscandia during the early Holocene are also reported in e.g. Kullman (1998), Luoto et al. (2014b) and Paus and Haugland (2017), and during early MIS 3 in Sarala et al.

(2016). The latter is inferred from findings of fossil remains of the aquatic taxa *Sagittaria sagitifolia* (14.4 °C), *Nymphaea* and *Callitriche* in sediment dated to MIS 3. Quantitatively inferred climate parameters based on fossil remains predating the LGM are scarce, not only in Fennoscandia but also on the European mainland. Warm summers as well as warm winters are recorded by plant macrofossils and insect remains at Oerel (northern Germany) during early MIS 5a (Behre et al., 2005).

4.6 Comparisons with studies in North America

One of the few detailed fossil analyses, including pollen, NPP's and macrofossils, on glacial lake sediments in North America is presented in Boyd et al. (2003). This study focuses on the terminal stages of Glacial Lake Hind, i.e. one of several interconnected proglacial lakes that formed across the Canadian prairies in front of the retreating margin of the Laurentide Ice Sheet in the early Holocene. Glacial Lake Hind discharged eastwards into Glacial Lake Agassiz (Fig. 1). Boyd et al. (2003) report a diverse macrofossil assemblage in glacial lake clays and silts, representing a high diversity of emergent and aquatic plants (e.g. various *Potamogeton* species such as narrow-leaved *P. filiformis*), and including abundant needles of *Picea* and a bud scale of *Populus*. Peak values for pollen of the wetland plant *Typha* in gyttja directly overlying the Glacial Lake Hind sediment indicates substantial postglacial warming (Boyd et al., 2003).

Early Holocene warm summers in response to Milankovitch-forced insolation have earlier been reported by Ritchie et al. (1983) based on pollen and macrofossil remains of *Typha* from 12 high-latitude sites in northern Canada dated to ca. 6-12 kyr BP and clustering at 10.5 kyr BP. The results from Canada are very similar to those obtained in the present study at Sokli indicating diverse aquatic biota, local presence of trees and warm summers along the retreating margin of the large N Hemisphere ice-sheets during deglaciation.

4.7 Glacial lake sediments and carbon storage

Although glacial lakes covered large parts of northern Europe and North America, contemporaneous glacial lakes generally were relatively small, confined to the deeper parts in the landscape. The glacial lakes went through complex evolutions as the topography changed and spill-ways opened-up along the retreating ice-margins (e.g. Dyke, 2004; Boyd et al., 2007; Johansson, 2007; Carrivick and Tweed, 2013). This is exemplified by the study of Jansson (2003) which mapped a total of 26 glacial lakes (65 sub-stages) in Labrador/Ungava, eastern Canada, during the early Holocene retreat of the Laurentide Ice Sheet.

Within the glacial lakes, protected bays were common features and, in combination with inflow of rivers draining unglaciated terrain, allowed for aquatic and telmatic biota to flourish in the lakes and along their shores (Boyd et al., 2003; Boyd, 2007; Bos et al., 2009; Helmens et al., 2009; Shala et al., 2014b; this study). Diverse biota was promoted by enhanced nutrient levels in the recently deglaciated terrain combined with insolation-induced warm summers. A close proximity to glacial plant refugia (e.g. Willis and van Andel, 2004) further facilitated the establishment of trees or open forest in the ice-marginal environment. Abundant macrofossils in the shallow glacial lake sediment of early Holocene age at Sokli, combined with the presence of birch forest in the catchment, led to an organic carbon content (LOI) in the sediment rising to 20 % (Fig. 4A; Shala et al., 2014a, 2014b). The sediment was found interlayered with thin organic laminae at a site close to the former glacial lake shore (Saunavuotso in Fig. 2B). This shows that postglacial carbon storage started within the glacial lake sediment, i.e. prior to the accumulation of peat that was initiated over large parts of central and eastern Canada (Dredge and Cowan, 1989) and northern Europe (e.g. Oksanen et al., 2001) due to the presence of the relatively impermeable glacial lake silts and clays. Although more regional studies are needed, the present study at Sokli reveals that aquatic biota and terrestrial vegetation quickly adapted to new environmental conditions during N-Hemisphere deglaciation and that glacial lake ecosystems, and the carbon stored in their sediments, should not be neglected in earth system modeling.

5 Conclusions

Our study shows that glacial lake sediments at the base of interglacial and interstadial deposits can provide important information on past environmental and climate conditions. These sediments have rarely been included in proxy-based palaeo-environmental studies, with the consequence that environmental and climate conditions during deglaciation of the large N-Hemisphere ice-sheets have largely remained unknown. Deglacial stages such as the LGM-Holocene transition are important testbeds in assessing climate sensitivity and the role of individual forcings and feedbacks in climate change (Shakun et al., 2012). In large parts of the N Hemisphere, the earliest evidence of the postglacial terrestrial and aquatic environments and climate are stored in glacial lake sediments. Our finding of distinct indicators of warm and productive conditions in the ice-marginal environment, immediately following deglaciation, is thus relevant for assessing the climate response and rates of ecosystem change during the critical glacial-interglacial transitions. Furthermore, the spatial extent and depth of glacial lake sediments, and their geochemistry, should be carefully assessed to quantify the carbon storage in glacial lake systems. Finally, paleo-environmental studies based on glacial lake sediments will benefit from studies in present-day ice-marginal environments, which, however, are currently scarce (Carrivick and Tweed, 2013).

Author Contributions

K.H. conceived the study and wrote the manuscript, with input from all authors. K.H., C.K., J.S.S., S.S., J.A.A.B., S.E., N.K., T.P.L. and M.V. performed laboratory analyses and, together with J.R. and J.W., made palaeo-environmental interpretations. A.O. made the glacial lake maps in Figure 1.

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Table 1. AMS radiocarbon ages for the MIS 5a lake (gyttja) deposit at Sokli.

Borehole	Depth (m)	Material	Age (yr BP)	Laboratory No.
Sokli 2/2010	9.4	<i>Macrofossils of terrestrial plants (mostly seeds of birch)</i>	>47000	Poz-56337
Sokli 2/2010	9	<i>Macrofossils of terrestrial plants (mostly wood)</i>	>51000	Poz-56338

Table 2. Mean July air temperature (T_{jul}) estimates based on macrofossils of aquatic/telmatic plants (minimum T_{jul} values) and chironomids (optimum T_{jul} values) for the different deglaciation episodes at Sokli. Present-day T_{jul} at Sokli is 13 °C.

Deglaciation episode	Minimum T_{jul} (macrofossils)	Optimum T_{jul} (chironomids)
Early Holocene	<i>Typha</i> (15.7 °C) <i>Glyceria lithuanica</i> (15.7 °C) <i>Callitriche cophocarpa/ hermaphroditica</i> (13.7-14.0 °C) narrow-leaved <i>Potamogeton</i> spp. such as <i>P. friesii</i> (13.6 °C) <i>Nymphaea</i> (13.5 °C)	<i>Cricotopus cylindraceus</i> -type (15.4 °C) <i>Cricotopus intersectus</i> -type (15.1 °C) <i>Chironomus anthracinus</i> -type (14.7 °C) <i>Polypedilum nubeculosum</i> -type (14.5 °C) <i>Microtendipes pedellus</i> -type (13.4 °C) <i>Psectrocladius sordidellus</i> -type (13.1 °C)
Early MIS 3	<i>Callitriche hermaphroditica</i> (14.0 °C) narrow-leaved <i>Potamogeton</i> spp. (<i>P. friesii</i> ; 13.6 °C)	<i>Chironomus anthracinus</i> -type (14.7 °C) <i>Cladotanytarsus mancus</i> -type (14.4 °C) <i>Polypedilum nubeculosum</i> -type (14.5 °C) <i>Microtendipes pedellus</i> -type (13.4 °C)
Early MIS 5a	<i>Ceratophyllum</i> (14.1 °C) <i>Callitriche hermaphroditica</i> (14.0 °C) <i>Callitriche cophocarpa</i> (13.7 °C) narrow-leaved <i>Potamogeton</i> spp. (<i>P. compressus</i> , <i>P. berchtoldii</i> ; 13.6 °C)	<i>Chironomus anthracinus</i> -type (14.7 °C) <i>Cladotanytarsus mancus</i> -type (14.4 °C) <i>Polypedilum nubeculosum</i> -type (14.5 °C) <i>Microtendipes pedellus</i> -type (13.4 °C) <i>Psectrocladius sordidellus</i> -type (13.1 °C)

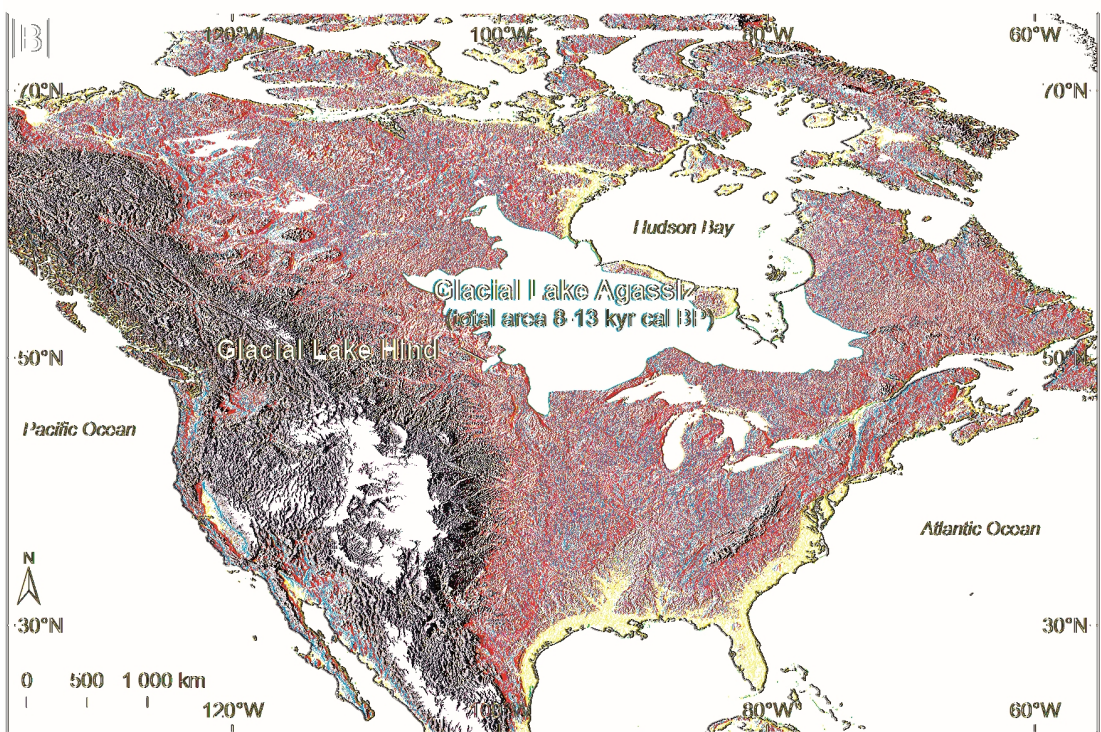
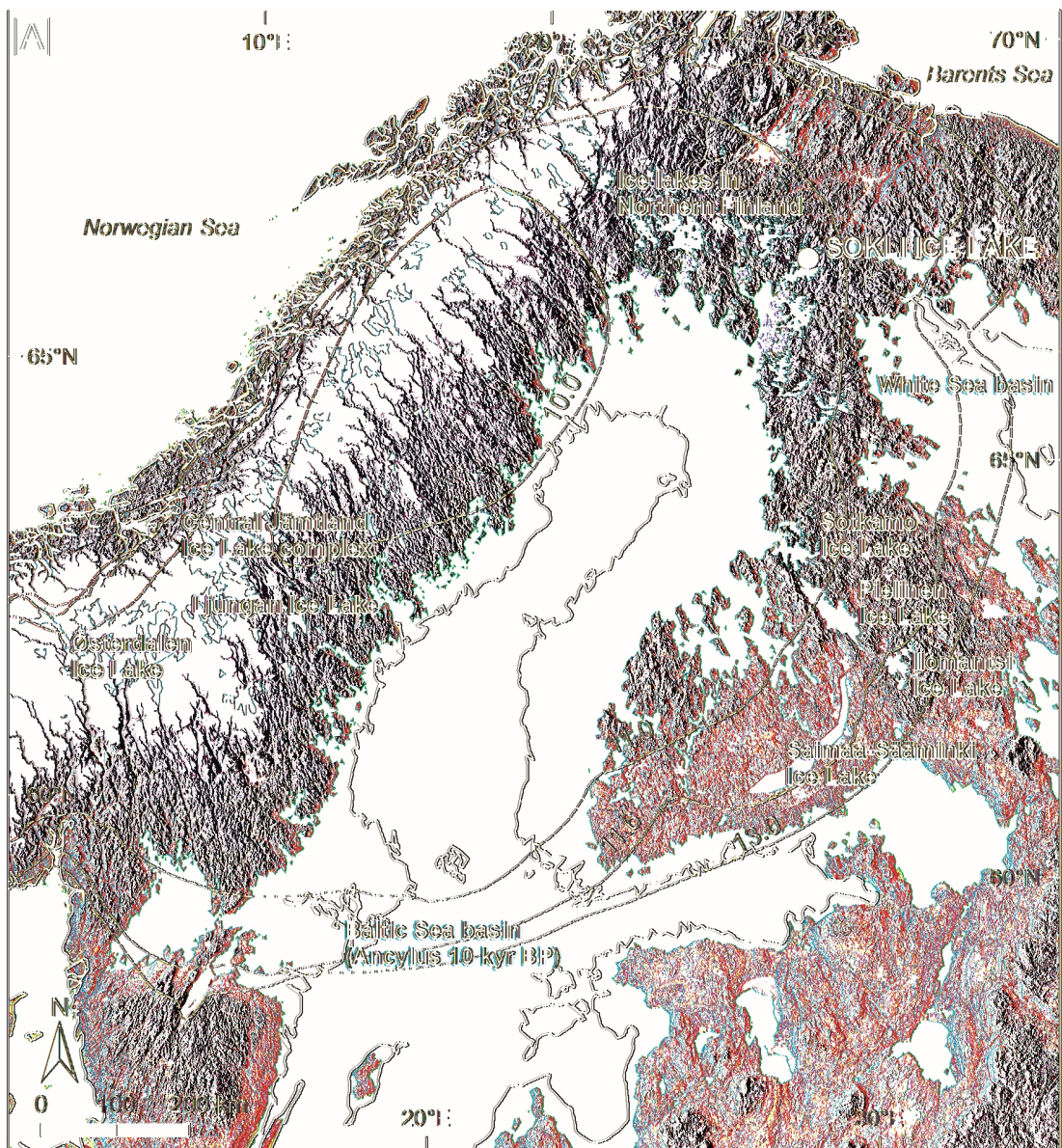
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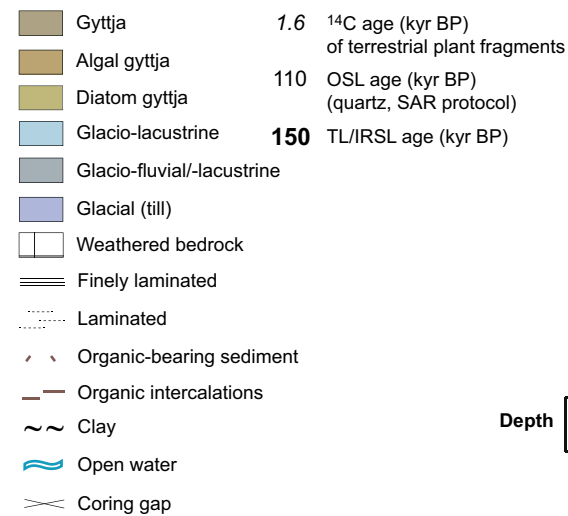
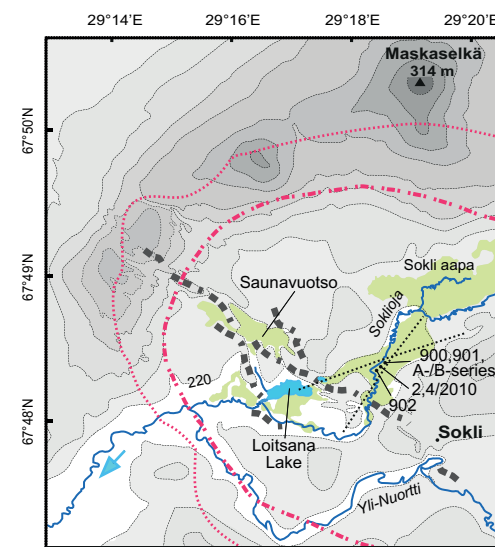
Fig. 1. The extent of glacial lakes in northern Europe (**A**) and North America (**B**) during the last deglaciation around 10 kyr cal BP. **A** shows the maximum extent of the Ancylus Lake in the Baltic Sea basin at 10 kyr cal BP (Björck, 1995). The other lakes are time-transgressive. The extent of Ice Lakes along the western margin of the Fennoscandian Ice Sheet, and the glacial retreat chronology, are according to Stroeve et al. (2016, and references therein), whereas Ice Lakes along the northern and eastern margin of the ice-sheet follow Johansson (2007) and Ojala et al. (2013, and references therein), respectively. The Sokli Ice Lake which is the subject of this study is highlighted. **B** shows the total cumulative area covered by Glacial Lake Agassiz in North America in the time interval 13-8 kyr cal BP (Teller and Leverington, 2004).

Fig. 2. **A** New composite lithological column for the Late Quaternary sedimentary sequence in the Sokli basin with to the right the local stratigraphy according to Helmens (2014). The location within the Sokli basin of boreholes which are indicated along the left side of the lithological log is given in **B**. The correlation of the Sokli record with the marine global oxygen-isotope stack (Lisiecki and Raymo, 2005) and high-latitude July insolation (Berger and Loutre, 1991) (**C**) is based on stratigraphy and absolute dating evidence (^{14}C , OSL, TL and IRSL dates); absolute dates are indicated to the left of the lithological column in **A** (see text). Deglacial sediment intervals that are the subject of the present study, dated to the early Holocene, early MIS 3 and early MIS 5a, are highlighted by pink boxes.

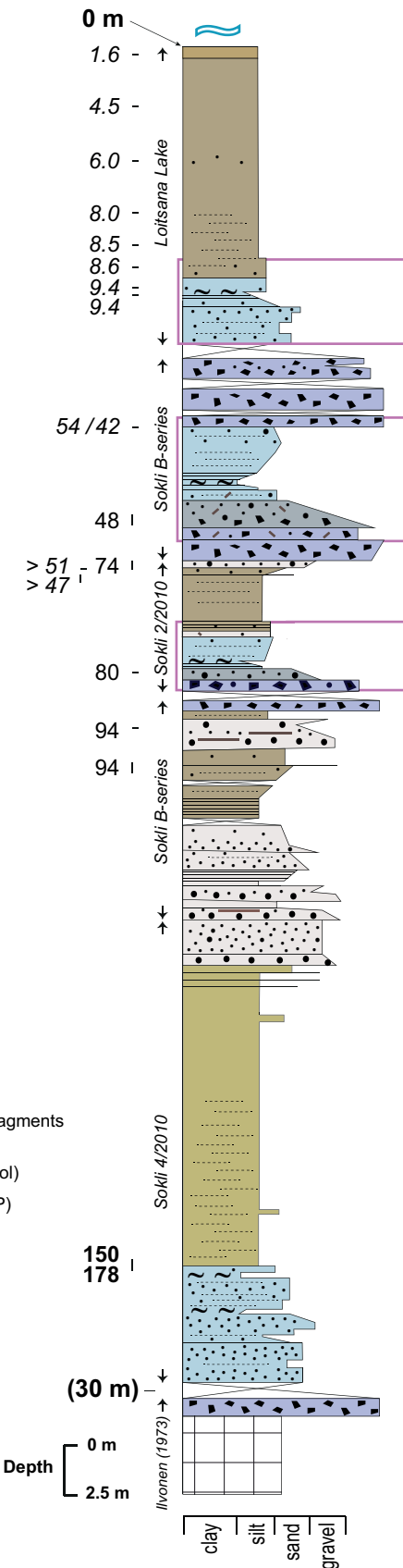
Fig. 3. Evolution of the later stages of the Sokli Ice Lake in the early Holocene; cross-sections show maximum water depths in Lake Loitsana (Shala et al., 2014a). Note that elevations are modern values. A similar glacial lake evolution occurred during the early MIS 3 and 5a deglaciation episodes. Lake Stage 1: deglaciation of the study site. Lake Stage 2: maximum spatial extent of the glacial lake. Lake Stage 3: partial drainage resulting in a smaller and more shallow glacial lake.

839 Fig. 4. Selection of proxy data for deglacial sediments in the Sokli basin dated to the early Holocene
840 (A), early MIS 3 (B) and early MIS 5a (C). For legends see C. Phytoliths and Tertiary diatoms are
841 calculated as percentages of the total sum of siliceous microfossils. Percentage values of pollen, spores
842 and NPP's are based on the total sum of pollen of terrestrial plants. Based on A Shala et al. (2014a,
843 2014b, 2017); B Engels et al. (2008), Bos et al. (2009), and Helmens et al. (2009); C this study.



B**A**

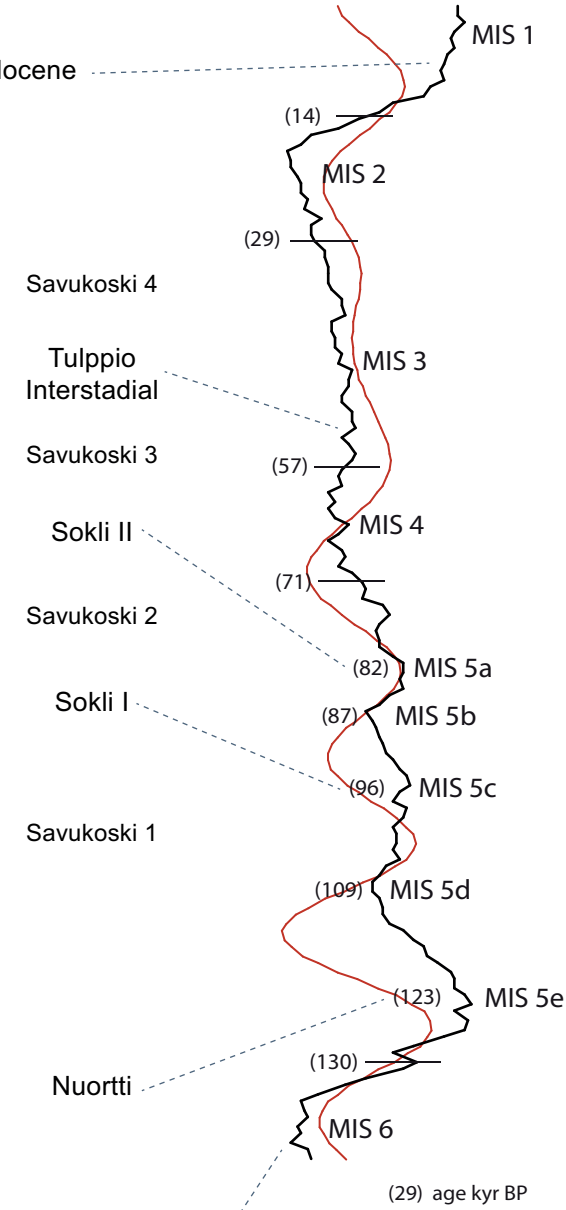
Composite log Sokli / Loitsana

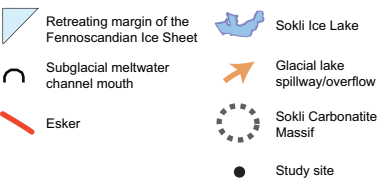
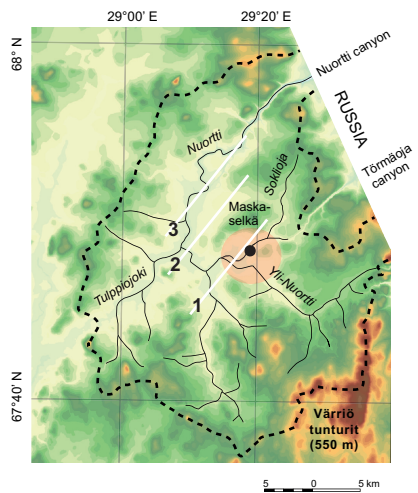
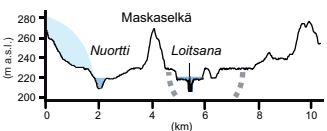
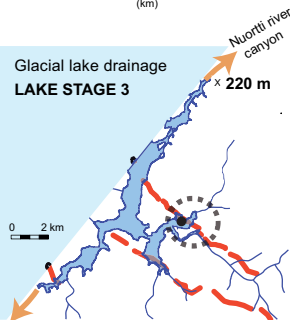
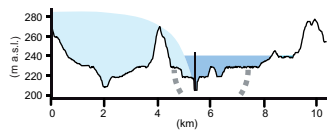
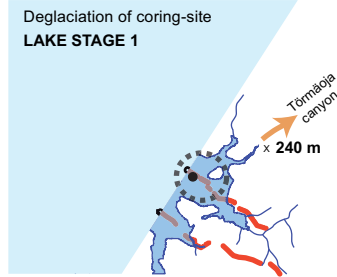
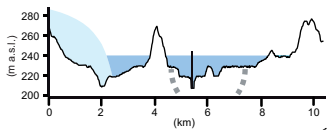
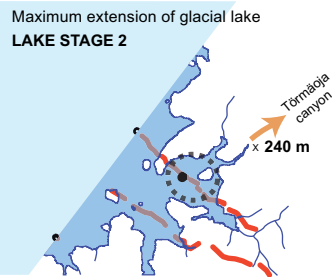
Stratigraphy
Sokli basin

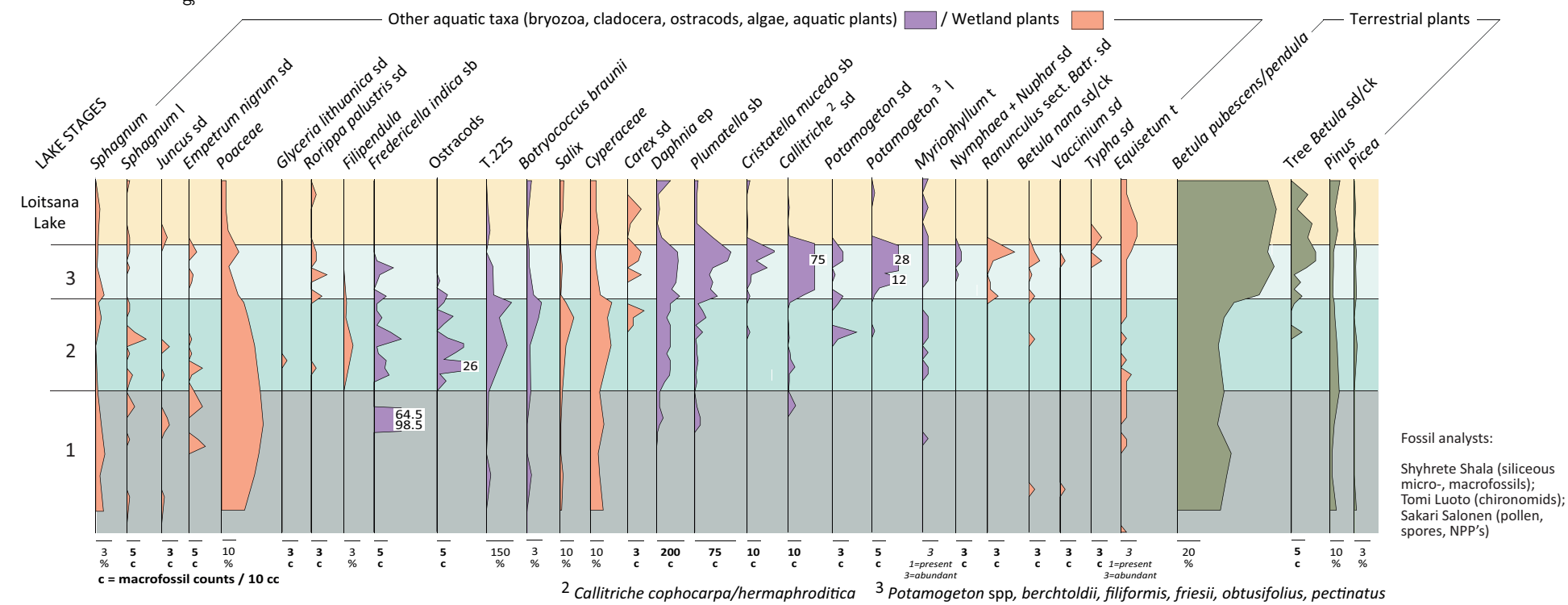
Holocene

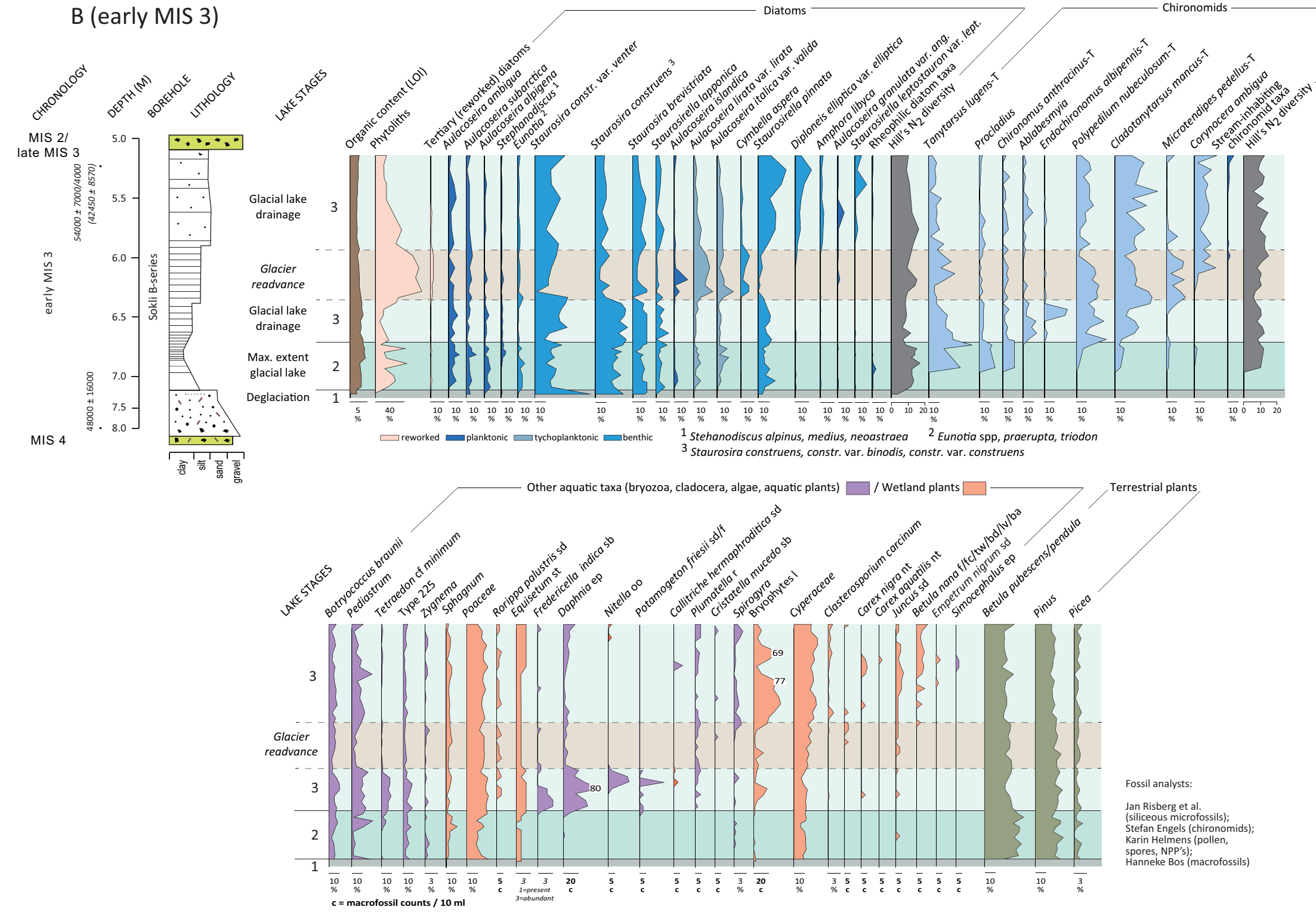
Last Glacial

Last Interglacial complex

Penultimate
Glacial**C**Insolation
July 65° N
Benthic $\delta^{18}\text{O}$
global stack
(LR04)



[illegible]



C (early MIS 5a)

